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JOURNAL

OF THE

New York Entomological Society.

Vol. V. DECEMBER, 1897. No. 4.

AN ATTEMPT TO CLASSIFY THE HOLARCTIC LEPIDOPTERA BY MEANS OF THE SPECIALIZATION OF THE WINGS.

PART I.—THE DAY-BUTTERFLIES.

By A. RADCLIFFE GROTE, A.M.

A. Forewings with vein IX present.....**PAPILIONIDES.**
a 1. Vein IV2 of primaries inclines to Cubitus .....PARNASSIIDÆ.
a2. Vein IV1 of forewings from Radius ..... PARNASSIINÆ.
d2. Vein IV1 of forewings from crossvein ..... THAIDINÆ.
a 1. Vein IV2 of primaries placed centrally .....PAPILIONIDÆ.
B. Forewings with vein IX wanting.....**HESPERIADES.**
b1. Radial veins on primaries not arising separately, or if separate less than five in number.
b2. Vein III4 to costa before apex.
b3. Wings not angulate.
b4. Vein IV2 not central on both wings.....PIERIDÆ.
b5. Vein III1 arising from above cell.....PIERINÆ.
b5. Vein III1 arising beyond cell.....LEPTIDIINÆ.
b2. Vein III4 to external margin below apex.....NYMPHALIDÆ.
b6. Vein II absorbed by III to junction with I on secondaries NYMPHALINÆ
b6. Vein II absorbed by III to a varying point but always before junction with I ....ARGYNNINÆ.
b2. Vein III4 to apex.
b7. Vein VIII not marked on primaries .....AGAPETIDÆ.
b8. Crossvein of secondaries joins Cubitus.....PARARGINÆ.
b8. Crossvein of secondaries joins vein IV3 .....AGAPETINÆ.
b3. Wings angulate..... .....LIBYTHEIDÆ.
b7. Vein VIII marked on primaries.
b9. Vein III2 beyond extremity of cell.....LIMNADIDÆ.
b9. Vein III2 before extremity of cell.....NEMEOBIIDÆ.
b4. Vein IV2 central on both wings.
b10. Vein I of hind wings developed.....RIODINIDÆ.
b10. Vein I of hind wings absent.....LYCÆNIDÆ.
b 11. Vein IV1 of primaries directly joining Radius ..... THECLINÆ.
b 11. Vein IV1 of primaries indirectly joining Radius... LYCÆNINÆ.

b1. Radial veins on primaries arising separately and five in number.
b12. Vein IV2 of primaries approaching cubitus.....MEGATHYMIDÆ.
b12. Vein IV2 of primaries placed centrally.....HESPERIADÆ.
b13. No costal vein (vein I) on primaries.....PAMPHILINÆ.
b13. A costal vein (vein I) on primaries.....HESPERINÆ.

The division of the Day Butterflies rests upon the presence of a strong and short downwardly curved vein at the base of primaries and joining the internal margin in the Parnassi-Papilionidæ, and its absence in all the other Day Butterflies. Whether we homologize this vein with the loop at the base of vein VII, which we call VIII, or give it a separate number the character is unaffected, for the loop runs in a contrary direction, and the opposite development of the vein in the Swallow-tails remains to be accounted for. But I cannot so homologize this peculiar vein and for several reasons. We find in *Castnia*, *Actias*, *Telea*, *Thyridopteryx*, a lower prolongation of the loop VIII. It seemed to me at one time that here might be a trace of this vein IX which would have anastomosed with VIII and finally have disappeared. But the greatest encouragement, that I might discover the phylogeny of *Papilio*, was offered me by the drawings of Mr. Meyrick in the Geometridæ. For here appeared vein VIII as a degenerate (dotted in the drawings) nervure, and, behold, IX was present likewise and indicated by a curved continuous line joining internal margin as in *Papilio*. Here I said, can I never be mistaken. This is the internal vein of the Papilionides. But when I, myself, tried to find Mr. Meyrick's vein in nature, it was not there. The pertinacity with which Mr. Meyrick repeats this vein in his drawings of the Geometrid wing leads one to suspect that he has really perceived it on some special occasion and now brings it in (*i. e.*, *Venilia macularia*) where there is no occasion. But I have small hopes.

The general resemblances, striking as they may be between the Hesperiades and Papilionides, or between *Papilio* and the rest of the Day Butterflies, might be all developed upon another line and the connection between the two would in that case be placed farther back still. Any system which places the Papilionides between the groups of the other Day Butterflies, all of which appear to me to hang more or less closely together, must first account for the fundamental neurational differences before it can be entitled to credit. The diurnal habit might be set down, with other features, to convergence.

There are two chief directions in which changes are making in the structure of the butterfly wing. The first is traceable throughout the order. Its aim is the breaking up of the system of theMedia, one

of the three primary veins. Its progress is not uniform, but is evidenced in different ways. The comparative completion of this effort affords a particular gauge of the standing of the form. The second direction occurs sporadically in very different groups. It consists in an absorption of the branches of the Radius, so that their normal number is diminished. It is probably reminiscent of what has taken place on the hind wings, as we see from *Hepialus*. When we apply our knowledge of these two tests of specialization to the Day-Butterflies, we find that the second, or sporadic direction, occurs in the Parnassidæ, Pieridæ, Lycænidæ, thus independently in otherwise very different groups. It is thus a secondary character and we find it again in a group so dissimilar to the Day Butterflies as the Saturniades, while it is not indicated in the Hawk Moths. The first or general direction of specialization we find indicated by most Lepidoptera, in some of its stages. It is a fundamental movement and has probably a mechanical cause. The Pieridæ unite the two directions in a palpable manner, more strongly so than the Lycænidæ, which exhibit, in the Theclinæ, the second direction very completely. In the Pierinæ (*Mancipium*, *Pieris*, etc.) the first direction is shown by the transfer of vein IV1, the upper branch of the Media, to the Radius. This state of affairs we find only again so strongly marked in *Nemeobius*. In the four-footed Butterflies the first direction, or suppression of the Media, asserts itself in the total degeneration of the crossvein; while the two upper branches of the Media are pulled towards the Radius, the cell opens completely. Thus the Media, as a system, ceases to exist. But in the Nymphalidæ, the upper branch of the Media does not become completely absorbed by the Radius, as in the Pieridæ, in which latter the cell is never so completely opened as in the former family. Again the *second* direction is not taken up at all by the brush-footed butterflies, the Radius remaining generalized, five-branched. Judging from the condition of the hind wings especially, the Agapetinæ and Limnadidæ are less specialized than the Nymphalidæ. The Libytheidæ overlap the more generalized Meadow-Browns. The neuration of the Libytheidæ is almost repeated by the Nemeobiidæ, which latter retain no essential wing characters of the Riodinidæ (Erycinidæ) or Lycænidæ. I tried to explain its position on the Lycænid branch by the view that the evolution of the neuration has taken a parallel direction to that of the Pieridæ and the four-footed Butterflies. On the neuration by itself we must, and I now do, exclude *Nemeobius* from the Lycænid branch. Its junction with this branch must remain

problematical. There are three patterns of the wings of Day Butterflies: the Papilionid, the Pieri-Nymphalid, the Lycæni-Hesperid. I cannot place *Nemeobius* satisfactorily because I am told it is a Lycænid while its wings are of the pattern of the Pieri-Nymphalids.

The plan of the Lycænid and Hesperid wing is identical. The first only differs from the latter, by the commencement of the absorption of the radial veins. It is, in my opinion, very improbable that the Lycænid and Hesperid wing should be separately evolved. The Lycænid wing is a continuation of the Hesperid and can be directly inferred from it. The process of absorption which divides *Lycæna* from *Hesperia*, makes a further step and produces *Thecla*. The morphological value of the stages is similar.

Although, from any limited study, the neuration appears as a whole fixed, it is not so; it has its flux, perhaps its reflux. A wider comparison brings this out already and it will bring it out more and more. The neuration has a present meaning which cannot be overlooked. To neglect or pass over its teaching, the conclusions we may derive from its variations, is to detract from the picture, to make this picture by so much an inaccurate one, of the present condition and the probable past and future of the organism. In the Lepidoptera, the veins which seem to be most stable are the main branches, the Radius and Cubitus. Perhaps the latter with its two branches is the more constant. The play is now with the Media and its system of branches. Even in so fast bound, so concrete a group as the Sphingidæ, where everything seems exhausted tending to a future development, where there is so little that is lax and pliable in any stage of the insect, the branches of the median system still shift, vein IV1 sometimes leaves the crossvein and appears attached to the Radius, while IV2 varies in its inclination to the Cubitus. So rigid and stark a neuration as we find in the Hawk Moths seems to defy the investigator and to tax his patience beyond its power. But finally even here something will be yielded to the diligent enquirer. He will be able on occasion at least to distinguish between the more generalized and the more specialized form and this through the veining of the wings. The wing of the Hawk Moths has assumed a certain stability from its meeting in a high degree the requirements of flight and holds fast to this pattern of veining in consequence.

The art of the student is exercised to seize upon what is disparate and bring these characters together into deeper harmony. No doubt, a record lies for us to read in the neuration of the wings; the difficulty lies in properly revealing it, in an adequate interpretation. What I

have called the "moving veins" appear to follow a still active law of development. Of the three primary veins, Radius, Cubitus and Media, the two main trunks have attained a certain fixity opposition through processes which have been carried on during an unmeasurable past. The criticism which our knowledge of the direction of the venation allows us of the recently published systems of classification is: that these are often founded on characters the relative value of which has not been ascertained, their recurring nature not taken into account. It is as though I had placed *Nemeobius* among the Pieridæ, because its pattern of venation demanded it, and then proceeded to erect a violent system upon such a basis after the fashion of Mr. Meyrick. But much better work will be done in working out all the variations in a single organ, endeavoring to bring out clearly the value of these variations and allowing the existing classificatory sequence, I might say the Linnéan sequence, as a rule, to stand. The work before us is still to make what is now difficult, easy. When we have reached this goal upon any point of our subject, there will arise plenty to take up the matter and display their penetration upon it further.

So we see that the principal gain from these studies is the attainment of a measure, a distinct register, of specialization. By it the groups and genera drop more naturally into their places. And these studies are critical of Mr. Meyrick's pretensions, who would arrange the Lepidoptera upon neuration but offers us a mass of incorrect figures, an impossible phylogeny and the proof positive that he has nowhere understood the movement of the veins. So, too, they reach classificators who blindly thrust the Swallowtails between the Blues and Hesperids, and they show that these also, have not even understood the conditions of the problem they assume to have solved with so much pomp of learning.

In Comstock's "Evolution and Taxonomy," to which work my indebtedness is very great, I find no distinct recognition of the two main directions of evolution in the wings as such, while there is everywhere apparent the laudable effort to correlate the changes with mechanical causes. The suppression of the Media is detailed on page 76. In this, my *first* direction, the movement of IV2 is thus discussed: "But in which direction would one expect the base of vein V2 to migrate? Occupying an intermediate position between radius and cubitus it may go either way. It is like a stream in the middle of a level plain, a trifle may change its course." The view taken by me is that there is a contest between Radius and Cubitus for the possession of the residue of the Media, after base and crossvein have degenerated. The two principal

veins are the residuary legatees of the branches of the Media, and the determining cause as to which shall succeed to the odd or middle branch lies in the habit of the insect in flight. The strengthening of the Radius implies a more sailing, that of the Cubitus a more hovering flight, with quicker up and down movement as in the Hawk Moths. Comstock distinctly regards the crossvein as established after base of Media has disappeared to hold the branches. I do not. The crossvein appears to me a residue which is next attacked after the base of Media has been absorbed. If the middle branch refuses to follow either Radius or Cubitus it falls away by want of a base of supply, as in *Lycæna* and *Hesperia*. (See "Evolution and Taxonomy," p. 70.) The axiom expressed by me: *The amount of the absorption is the measure of the specialization*, is intended to embody the leading principle which is to guide our pterogostic studies.* In the Pieridæ alone have I found both positions of IV2 expressed. While in *Leptidia* the position on secondaries is cubital, in all the rest of the genera it is radial. I follow Comstock's general view in considering this as here indicating dichotomy of descent and establish upon it a subfamily division.

To summarize the principal openings through which I have tried to carry the working theory of the evolution of the wings beyond what had been previously attained:

1. I try to show that the suppression of the Media is the result of a continuous movement which, after absorbing the connection of the system with the base of the wing and thoracic sources of supply, next disintegrates the crossvein and distributes the branches between Radius and Cubitus. It is probable that the crossvein is an old character, an adapted survival of a former system of crossveins.

2. That that part of the crossvein closing the cell, and lying between the median branches and either Radius or Cubitus, becomes functionally the base of the branches in their new auxiliary position after the disintegration of the central or connecting portion of the crossvein. Its former morphological character as a portion of the crossvein becomes gradually lost, the angles rounded off.

3. The absorption of the radius branches is sporadic on different lines of descent and is a reminiscent action of the absorption on the secondaries which has here already generally fully taken place and been

*The inequality of the specializing movement has been recognized by me in various places: Die Saturniden, 11, etc. The correlation of flight with the portion of the middle branch of Media is endeavored to be established by me in the "Tagfalter," etc., pp. 4 and 5.

carried to its extreme. I try to show, in pursuance of this observation, that it is questionable whether we can believe that the corresponding simplification can be attained by the Radius of the primaries, from the different position and conditions of the two wings. It is also interfered with by the absorption of IV1. This proves the absorption of the Media to have commenced after the absorption of the radial veins on secondaries.

4. I try to show that the general movement is inaugurated with the secondaries and that these show its effects more plainly than the primaries in one and the same individual. We must logically expect this to be the case from the entire course and the resulting theory of the specialization as applied to the wings, and regard it as arising from mechanical causes.

To descend to the application of these conclusions to classification, I try to show:

1. That the position assigned by Scudder and Comstock (l. c. III,) to the Swallowtails, next above the Hesperidæ, cannot be maintained in view of the pattern of the wings. The wing pattern of the Hesperiadæ and Lycænidæ is really the same and the interpolation of the Papilionidæ at this point is a violent proceeding. Far better is the position assigned to the Papilionidæ by Chapman; best of all the placing of the Parnassi-Papilionidæ, in a linear series, at the commencement of the Day Butterflies. The longitudinal vein IX on primaries, being a subprimary vein offers a subprimary character for dichotomy. The wing of *Papilio* loses its generalized characters, by a gradual process of specialization, in *Parnassius*. The Parnassi-Papilionidæ differ by a "high" character, the loss of VIII on secondaries, from all the other butterflies. They are thus comparable with the Attacinæ, the most specialized of Moths.

2. I have shown the indissoluble nature of the alliance between the Parnassiidæ and Papilionidæ and that the former are more specialized and should "head the series." The similiarity in color between the Parnassians and Pierids is adventious and secondary.

3. I have shown that the Nymphalidæ retain the radius in a generalized condition. That the higher groups alone show a perfection on on the opening of the cell, but that the upper branch of the Media is not absorbed by the Radius (as in *Mancipium*, *Pieris*, *Nemeobius*) but retains generally its position on the crossvein at the extreme upper corner of the cell. I thus show that there is small ground, from the neuration, for any supremacy of the Nymphalidæ, still less of the Agapetidæ,

or Limnadidæ, which are distinctly less specialized than the Nymphalidæ proper. So that we see that the statement of the Editor of the Philadelphia "Check List," that, in his "opinion," the Nymphalidæ are "correctly placed at the head of the Rhopalocera" is not derived from what this writer elsewhere calls "scientific knowledge" or "science," but is plainly the result of an effort to get into good company. It is characteristic also of this sort of "opinion," that when we turn to the List itself we find it to "head" with the Limnadidæ, the most generalized of the four-footed Butterflies. The success of the Nymphalid branch in attaining a variety of forms and a vast array of species has been great, and this tends to our believing it to he so dominating. It is, however, lateral, not on the main line. In the accompanying diagram the opening of the cell has led me even to give the higher groups perhaps too exalted a position, but this is a minor point. The connection of the Charaxini, a foreign group, with the main stem of the Nymphalidæ is problematical. I have commented on its position elsewhere, and it must be brought into place when the tropical butterflies are studied upon the basis here set forth.

4. It may be further assumed, that, in former periods of time, the grouping was laxer than to-day, and that the families we now are able to separate were once interconnected by forms which have dropped out. At that time the four or brush-footed butterflies may have been more nearly connected with the six-footed stem. From small and specialized groups we cannot expect the birth of new features, but from large and spreading assemblages, presenting a wide range of character. That such a state of affairs existed in the Whites, we have the testimony of *Leptidia* to prove. This butterfly appears now as an isolated survivor of what was probably a large group of Pieridæ. The abyss separating *Leptidia* from the Pierinæ is profound and I am informed that even more important deviations still exist in the family. The Pierids may then well represent the matrix from which the four-footed type proceeded.

5. Boisduval's groups of Suspensi, Succincti, Involuti, based on the fashion of fastening the chrysalis, have no existence as phylogenetic assemblages, hence are improperly used in this manner by Mr. Scudder. The Papilionid, Pierid and Lycænid Succincti have clearly reached the habit independently. It is a fallacy to believe, with Mr. Scudder, that there is a regular progression from the cocoon of the moths to a total absence of the use of silk. Instances are not rare where the generalized forms spin little or no silk and the specialized forms on the same phyloge-

netic line, make large and complex cocoons. This envelop to the pupa is so clearly an adaptive secondary character, that in one, single, upon all other characters, homogeneous group, like the Emperor Moths, the habit runs through the entire scale, from utter absence to a specialization hardly elsewhere attained, the hanging cocoons of *Philosamia*, *Attacus* and *Callosamia*. Only on paper does the sequence seen by Mr. Scudder exist. The specializations of the butterfly do not keep pace with Mr. Scudder's imaginary series, *Pieris* is more specialized than *Nymphalis*, and *Nymphalis* than *Oeneis*. The differences in the mode of attachment are brought by Mr. Scudder into an artificial connection. As to the "shrouds" of the Involuti, the utmost we can grant to Mr. Scudder is, that the mode of attachment in *Hesperia* may represent a stage by which the cocoon-making larva prepared itself to abandon this habit. To make more of the observation than this is to trifle. In a similar way the fact that in *Thais* the girdle has slipped up to the "nosehorn" may figure a stage between the Succincti and Suspensi. But *Parnassius* does not follow this lead. Among the Agapetidæ, *Oeneis* is a generalized form. The most specialized Satyrids, I have met with, are *Pararge* and *Lasiommata*. In these vein IV_3 of the hind wings has effected its junction with the Cubitus. But in *Oeneis œllo* this junction is not attained and vein IV_3 springs still form the cross vein as in the mass of the more generalized forms. *Oeneis* belongs evidently to the genera allied to *Erebia*, in which vein I is developed, curved and running to a point. Herein it departs from *Eumenis*, in which this vein is blunt as in the Pararginæ. The character of IV_3 offered by *Oeneis* is important. It shows that this vein has not been fully absorbed by the system of the Cubitus, in this genus and the whole subfamily, Agapetinæ, to which *Oeneis* belongs. From a study of the imago, Mr. Scudder's classification is thus clearly to be rejected. The view that the Lycænid Succincti are specializations of the Papilionid is clearly an imaginary one.

6. The sequence in the above table is that recommended by me to be followed in catalogues and collections. The tribes are omitted because they are not sharply divisible. They are more or less lax groupings of allied genera near extensions of the generic idea. Each family or superfamily commences with the more specialized forms. To reverse this order in collections or catalogues is, I believe, impracticable from the nature of the objects here studied.

EXPLANATION OF DIAGRAM.

A. Papilionid stem (Papilionides) characterized by the presence on forewings of vein 'IX;' *B*, Hesperid stem (Hesperiades) characterized by the absence of the same vein. The titles of groups in *italics* denote that in these a reduction of the radial branches occurs (specialization through the *second* evolutionary movement). All the groups are arranged with regard to the specialization of the wing in the two principal directions. The *first* direction lies with the breaking up of the system of the Media and the final redistribution of the outlying three branches between the Radius and Cubitus, and this reaches a culminating point in the disintegration and disappearance of the cross vein (Nymphalinæ). In the Moths the same phenomenon is repeated in the Attacinæ (*Rothschildia, Samia, Philosamia, Callosamia, Attacus.*); IIa is the six-footed Pierid and main branch; IIb the four-footed (brush-footed) Nymphalid branch; both have the same essential wing pattern, or style of distribution of the veins and this is shared also by IIc, the Nemeobiid branch. IId is the Hesperid main branch; IIe the Lycænid specialized branch; IIf is the Hesperid generalized branch. The pattern of IId, *et seq.*, differs from the Pieri-Nymphalid branches by the simpler, more equidistant veining. The specialization, in the *first* direction, displays itself here by the disintegration of the cross-vein without a shifting of the outer branches, which latter remain *in situ.*

NOTES ON THE LARVA OF LAGOA PYXIDIFERA.

By HARRISON G. DYAR.

Since Abbot & Smith's work, in 1797, there has been no original reference to the larva in literature. It may be fitting that the one-hundredth anniversary of the discovery of the larva should be celebrated by a brief redescription, especially as Abbot & Smith's figure is somewhat erroneous and misleading. Their figure gives the impression of a longitudinally banded larva, whereas it is really uniformly colored. The larvæ occurred to me in some numbers at Miami, Florida.

Feet and warts, as usual in the genus, distinct; head retracted. Body slate gray; hair dense, concealing everything, regularly directed backward, soft, smooth, pale whitish gray with an under tint of darker gray which predominates narrowly along the subventral edge and in a disheveled anterior tuft above the hood. Dorsal line slightly keeled; anal hair short; no tufts. Anal plate reddish. In the earlier stages the hair is thin and fluffy, white; but the body shows through sordid whitish with a brownish dorsal band divided by a pale line and a broad brown lateral band. The spiracular glands show white. Edge of cervical shield and anal plate orange tinted. Cocoon and pupa as in *L. crispata.* Feeds on the young shoots of live oak. The larva differs from that of *L. crispata* only in color.

DIAGRAM OF THE PROPOSED DIPHYLETIC GENEALOGICAL TREE FOR THE HOLARCTIC DAY-BUTTERFLIES.